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par Monsieur Jean-Pierre SIGNORET

Sujet de la thèse : CONTRIBUTION A L'ETUDE DES MECANISMES ETHOLOGIQUES ET ENDOCRINIENS DU COMPORTEMENT SEXUEL DE LA TRUIE (Sus Scrofa L.)

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Swine Behavior in Reproduction

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Modern trends in animal husbandry are leading to what appears as a complete disassociation between the spontaneous animal's way of living and the sophisticated techniques of management for superior growth rate and feed conversion. So, we may question whether it is not only useful but even possible to discuss animal behavior under such conditions as those of modern animal breeding.

In the wild, for each type of behavior, more or less elaborate patterns take place in a social structure with preestablished interindividual relations, and in a wide home range. Oppositely, the need for an accurate control of environmental conditions, the necessity to simplify the care of animals, the problems of market, etc., result in a reduction of square feet per animal and force a drastic change in feeding and social relations from the natural ones.

In the field of reproduction, artificial insemination is a useful tool for the use of the better strains for genetic improvement, whereas in the female, estrus control allows planning of farrowing and, with early weaning, more intensive use of the reproductive capacities.

The fact that the pig is able to survive and reproduce under such conditions supposes a series of behavioral characteristics allowing and facilitating this adaptation. Among such characteristics reviewed by Hale (1969) the most important concern social and sexual behavior.

1. *Promiscuous mating* and the absence of pair-bond formation. Any female can be mated to any male.

2. *Simplification* of the patterns of sexual behavior. The sexual signals provided by movement or postures, and able to release copulation rapidly instead of more elaborate signals and long-lasting patterns involving rituals for establishment of social relations in preparation for the actual mating.

But, if the patterns of behavior were allowing domestication, we do know that the "natural" patterns are eliminated, even after hundreds of years of changes in the conditions of life. The unique stability of behavioral patterns appeared in dogs (Scott, 1954), fowl (Banks, 1956), sheep (Grubb and Jewell, 1966) and pigs (Fradrich, 1965; Gundlach, 1968). Strain differences in behavior may be selected as useful for the adaptation to domestication (tameness in foxes Trut and Belyaev, 1968). Such a variability takes place, however, inside the behavioral repertoire of the species and involves generally minor features.

So, the study of behavior may be of some use in modern animal husbandry in two respects:

1. *To determine* how far it is possible to change the so-called "natural" condition of animal life, to use the plasticity of adaptation of the species without impairment of the economy of production.

2. *To use some* behavioral traits in developing or adapting techniques of management, housing, feeding or reproduction.

This report will be in three parts:

1. *A review* of the patterns of sexual activity in this species.

2. *An analysis* of the physiological and ethological mechanisms of sexual behavior.

3. *The relation* with the practical problems of pig reproduction.

The Patterns of Sexual Activity in Swine

The Male

Puberty

The boar reaches physiological puberty as early as 110 to 125 days, as spermatozoa were found present in the testes at this age (Andrews and Warwick, 1949; Hauser *et al.*, 1952). But there is some delay before gametes are able to fertilize the ova (Wiggins *et al.*, 1951).

As in several other mammalian species, some patterns of sexual behavior can be observed in young animals, as a part of play behavior. Mounting can be observed very early, even during the first 10 days of life, but later on it occurs frequently in groups of males. After the age of 4 months, it may be accompanied by erection (Grauvogl, 1958). The coordinated pattern of sexual behavior toward estrous females has not been observed before 5 months of age.

Generally the first ejaculation occurs when the boar is between 5 and 8 months old (Niwa and Mizuho, 1959). Such data agree with the observations of Wiggins *et al.* (1951), Hauser *et al.* (1952) and Lagerlof and Carlquist (1958). A better coordination of sexual behavior patterns can be acquired. For instance, mounting of the forequarters, rather commonly observed in young boars, disappears in sexually experienced animals.

Mating

Precopulatory patterns—The boar generally mounts the estrous female very rapidly. Schenk (1967) observed that only 17.4% of fully receptive females are not mounted immediately when presented to the male. Sumption (1959) noted that ejaculation begins within 200 seconds in 54 out of 70 tests. In our own records of

202 matings, the average mount latency was 43 seconds.

Some boars mount and dismount several times before actual coitus but generally the male does not dismount before the end of copulation. Erection occurs only after mounting. Wierzbowski and Wierzchos (1968) observed an average interval of 82 seconds between mounting and erection (219 ejaculations).

Intromission and ejaculation—After mounting, the boar thrusts until the tip of the penis is partially unsheathed and then penetrates the vaginal orifice. After some more thrusts, ejaculation begins. During this phase, the male's haunches are clenched together and pressed forward. Several additional thrusts can be observed during mating but at the time of ejaculation itself the boar is generally immobile. A muscular wavelike movement of the perineum is visible and one of the testes may be retracted.

Generally, the end of copulation is caused by dismounting of the boar. The female sometimes moves at the time (18% of the cases observed by Schenk, 1967) but this seldom disturbs ejaculation.

Among farm animals, the boar has the longest ejaculation time with an average of 4 to 6 minutes (Burger, 1952; Bascos, 1953; Wierzbowski and Wierzchos, 1968). In our observations of 438 matings, the average duration of copulation was 4.70 minutes.

Mechanisms of ejaculation—Stimuli which cause ejaculation appear to be essentially tactile. Fixation of the penis, spiral-shaped in the cervix, seems of major importance. Temperature stimuli are not necessary.

Exhaustion tests—When the boar is allowed free access to a female during the estrous period, several copulations occur: 7-11 with an interval between matings ranging from .2 to 15.4 hours (Burger, 1952), 4–8 (Quinto, 1957) or an average of 6.6 (Bascos, 1953). The highest frequency of ejaculation in this species is cited by Jakway and Sumption (1959)—8 ejaculations in the course of a 2.25-hour test with 9 estrous females available.

The Sexual Activity and Its Variations

Estimation of the sex drive—The sexual behavior of the boar has not been studied with accurate techniques and observed in detailed mating tests. The reaction time, or mounting latency, was recorded in several studies but this measure proved to be, in other mammalian species, insufficient for scientific approach, being highly variable according to the environmental conditions and the male's previous experience.

Factors of variation in sexual activity—**Age.** An increase in the reaction time was observed in the records of the experimental center of the French Agricultural Research Institute I.N.R.A. but although the number of spermatozoa and the volume of the ejaculate increase during the first 18 months of life, the duration of ejaculation does not change (Table 1).

Season. A high environmental temperature appears to have an adverse effect on the sexual activity of the boar (Niwa and Mizuho, 1954; Burger, 1952; Grauvogl, 1958) but in the moderate climate of western France no seasonal variation can be observed in reaction time, duration of ejaculation, sperm volume and composition (Table 2).

Influence of mate. The presentation of a "new" estrous female was successful in enhancing the boar's sex drive after copulation. Up to five copulations were obtained from one male in 75 minutes with six estrous sows (Jakway and Sumption, 1959).

Mate preference or aversion was noted by several authors. Hodgson (1935) cited a refusal of mating between sibs of inbred strains. Burger (1952), Jakway and Sumption (1959) and Grauvogl (1958) have observed similar aversion or preference of some females to specific boars.

Individual variations. In our own records (Signoret, 1969), the average individual mount latency ranged

Table 1. Evolution of sex drive and semen composition with age of boar.

Age (years)	1	1–1½	1½–2	2–2½	2½–3	3–3½	3½–4	4–4½	4½–5	5–5½
Number of ejaculates	97	475	525	529	398	368	363	231	172	87
Av. mount latency (min.)	0.7	0.8	0.9	1.0	1.4	1.5	1.4	1.6	1.4	2.0
Av. duration of ejaculation (min.)	5.6	5.8	5.8	6.3	6.3	5.3	5.5	5.4	5.9	5.9
Av. volume of semen (ml.)	254	258	307	313	323	290	314	295	300	284
Total number of spermatozoa (x109)	88	91	105	104	107	106	99	96	95	92

Experimental A.I. Center—I.N.R.A., Rouillé (86), France.

Table 2. Seasonal evolution of sex drive and ejaculation in boars.

Months	Jan.	Feb.	March	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.
Number of ejaculates	262	261	310	270	277	272	270	259	244	272	275	281
Av. mount latency (min.)	1.1	1.4	1.3	1.3	1.1	1.2	1.2	1.3	1.2	1.1	1.0	1.2
Av. duration of ejaculation (min.)	6.4	6.0	5.8	5.8	5.6	5.2	5.8	5.3	5.3	5.6	6.1	6.5
Av. number of spermatozoa (x109)	99	98	98	94	99	100	93	103	108	107	104	99
Av. volume of semen (ml.)	289	271	272	281	300	309	295	301	308	324	329	339

Experimental A.I. Center—I.N.R.A., Rouillé (86), France.

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Table 3. Physiological stage of gilts slaughtered between 90 and 110 kg.

Stage	Ovary	Uterus	Number of cases observed	Percentage
Infantile	Numerous follicles. Diameter 2–3 mm. No follicles larger than 5 mm.	Thin-pale. Av. weight 30 g.	92	10.7
Impuberal	id.	Thicker-pink. Av. weight 60 g.	289	33.7
Prepuberal	5–20 follicles. Diameter 5–8 mm.	About adult size. Thick-pink. Av. weight 150–250 g.	212	24.7
First ovulation	Recent ovulations No regressed corpora lutea	Thick-dark-pink. Av. weight 250–300 g.	36	4.2
First Cycle	Active C.L., but no regressed C.L.	id.	96	11.2
Cyclic	Active C.L. or large follicles and regressed C.L.	id.	133	15.5

from 19 to 119 seconds and the duration of ejaculation from 3.3 to 7.5 minutes. The genetic control of the patterns of sexual activity is evident when clear-cut differences between breeds or strains are demonstrated. Hauser *et al.* (1952) reported differences in sex drive between several strains. Wiggan (1961) found that Hampshire boars ejaculated twice as frequently as Minnesota Number Ones and Yorkshires. Strain differences in the duration of ejaculation are cited by Burger (1952) and Smidt (1961).

Territory. Several authors note an impaired sex drive when the boar is out of his home pen (Tillman, 1953; Krallinger, 1933) but such a reaction appears to be a consequence of the unfamiliar environment, rather than a territorial behavior such as described in cats and rabbits.

The Female

Puberty

Puberty generally occurs between 6 and 8 months of age. Breeds differ in this respect and heterosis is expressed by earlier maturity of some crosses (Foote *et al.*, 1956; Zimmerman *et al.*, 1960). Gilts born in spring reach earlier puberty than those born at other seasons (Wiggins *et al.*, 1950; Robertson *et al.*, 1951a; Gosset and Sorensen, 1956). The level and the balance of nutrition appear to influence the age at first estrus (Gosset and Sorensen, 1959; Robertson *et al.*, 1951b; Salmon-LeGagneur, 1970, etc.).

As puberty is approaching, some ovarian follicles are growing and the genital tract enlarges. A stage of "prepuberty" was described by Du Mesnil du Buisson and Signoret (1962). Whereas most ovarian follicles have regressed, a small number of them develop up to a diameter of 6-8 mm. Simultaneously, the uterine weight is similar to that of mature females. From figures obtained in slaughterhouses among gilts of 90–110 kg. live weight, the percentage of animals at this stage reaches 212/858 = 24.7%. At this moment puberty can either occur spontaneously or may be triggered by external influences (Table 3).

Normal ovulation takes place at first estrus and fertilization rate is good. In an experimental group of 126 gilts inseminated at the first estrus detected by the boar (average: 214 j.; average weight: 112 kg.), 86.1% were pregnant (LeGault, Ollivier, Du Mesnil du Buisson, Signoret, 1970, unpublished data). Nevertheless, some prepuberal gilts exhibit sexual behavior patterns such as mounting but they never allow being mounted by the boar (Schmidt and Breitschneider, 1954; Ito *et al.*, 1960).

Delayed puberty sometimes occurs in some herds. Salmon-Le-Gagneur (1970) and Martinet *et al.* (1970) cited herds where hardly 50% of the gilts had their first estrus before one year of age.

Estrus

Signs of estrus—The onset and disappearance of estrus is gradual in the pig. As estrus approaches, the sow is restless, frequently sniffs at the genitals of her pen mates and will ride the others or be mounted. Mounting behavior begins the day before actual receptivity in 2.8% of the sows, is observed respectively in 18.1, 38.7 and 16.8% of animals on the first, second and third days of estrus, and reduces to 3.5% on the first postestrus day (Holtz, 1967). She often utters typical grunts (Grauvogl, 1958; Holtz, 1967). Spontaneous activity may reach twice the normal level (Altmann, 1941). Appetite is often capricious.

Swollenness and coloration of the vulva are observed 2–6 days before the actual onset of estrus. Sometimes such signs last up to the end of receptivity but often they disappear during or even before acceptation of copulation (Burger, 1952; Willems, 1961; Ito *et al.*, 1960; Hansen *et al.*, 1960; Tchudnovsky, 1960; Holtz, 1967). Holtz (1959) has observed however that only 75% of the sows exhibit noticeable changes of the vulva at the time of estrus. Cyclic changes in vaginal smears can be observed. The clearest is an increase in the percentage of leucocytes that takes place at the beginning of sexual receptivity. (Altmann, 1941; Holtz, 1967).

Basal body temperature changes are reported to occur at the time of estrus (Altmann, 1941; Sanders *et al.*, 1964; Holtz, 1967).

Mucous discharge from the vulva is often reported to be more important at estrus. But none of these signs are reliable enough to be used as objective tests of heat. Arborization of cervical mucus (Betteridge and Raeside, 1962) and drop in vaginal pH (Schilling and Rostel, 1964; Holtz, 1967) are reported to be better physiological indicators of estrus.

Duration of estrus—The period of acceptation of copulation lasts an average of 40 to 60 hours (Burger, 1952; Smidt, 1965, Ito *et al.*, 1960; Schmidt and Breit-

Table 4. Seasonal variation in estrus duration.

Season	Number of cases	Average duration of heat (hours)
Winter	365	52.98
Spring	369	54.75
Summer	515	58.85
Fall	439	56.83

schneider, 1954; Hof, 1956). In our records of over 2,500 estrus in Large White gilts, the average is 53.13 hours ± .36 (with a range from 12 to 120). The first estrus is shorter than the others (47.2 vs. 55.8 hours) (Signoret, 1967a) and the sows have a longer receptive period than the gilts (Burger, 1952; Ito *et al.*, 1960). Breed differences are cited by Burger (1952) (68.2 hours for Large Black vs. 49.9 for Large White). In our records the individual duration of heat is repeatable from one estrus to another and a seasonal variation appears (Table 4).

Burger (1952) found no diurnal pattern in the onset of heat.

A significant influence of the number of ovulations appears in the analysis (Signoret and Land, unpublished data 1970), with an average of .454 C.L./day.

Moment of ovulation--Ovulation is generally reported to occur during the second half of estrus. This is confirmed by direct visualization of the ovaries by coelioscopy (Du Mesnil du Buisson *et al.*, 1970). The ovulation takes place between 38.47 and 42.27 hours after the onset of estrus and its average total duration is 3.8 hours (Fig. 1).

Sexual cycle

The length of the normal estrous cycle is reported to be 21 days. This is confirmed by the average value obtained in our observations (21.31 ± 0.57--1,780 cycles) but the mode of the distribution is 20 days. So considering as "normal" the cycles of 20 ± 10 days, the average is 19.91 ± 1.77 (94.5% of the cycles recorded). Once estrous cycles begin, heat occurs regularly unless the sow becomes pregnant. Although fragmentary evidence suggests that a sudden change in management may have a consequence on the cycle, this has not been proved in detailed studies.

"Silent" estrus--It is possible to consider a silent estrus as having occurred in cycles ranging from 36 to 45 days. Records of Burger (1952) show that this occurs in only 1.49% of the cycles. In our own records, 38/1,780 cycles (2.1%) fall in this range.

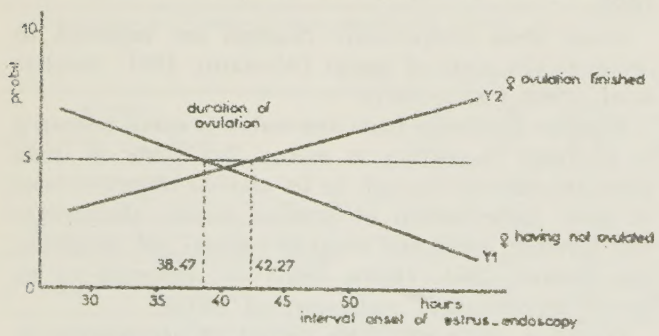

Fig. 1. Evolution of ovulation in the sow.

Table 5. Influence of mating or insemination on the duration of estrus.

Conditions	Number of cases	Average duration of estrus (hours)
Mating	46	55.83 ± 0.47
Artificial insemination	162	55.92 ± 1.92
Estrus detection by the boar	1,478	55.37 ± 1.05

"Split" estrus--The initial presence of estrus behavior followed by a nonreceptive state and a further receptivity is sometimes reported but it proves to be exceptional when heat detection is carefully done (2 cases in 1,109 observations, Burger, 1952).

Behavior of intersexual females--Intersexuality without abnormal external genitalia that can be observed in .1 to .2% in the Large White breed leads to a state of permanent sexual interest--sniffing of pen mates' genitals, mounting and interest in males. Seldom do they allow mounting of the boar.

Patterns of Sexual Activity in Relation With Copulation, Gestation and Lactation

Copulation--Estrus duration is apparently not affected by mating or artificial insemination (Burger, 1952; Signoret, 1967) (Table 5) although other authors report a shorter heat after mating (Lebedev and Pitkianen, 1951; Grauvogl, 1958).

After unsuccessful mating or insemination, the rate of "abnormally" long cycles (over 45 days) increases to an average of over 10% compared to less than 3% without mating or insemination (46/1,780 cycles = 2.6%). A seasonal variation appears. The "abnormal" or delayed return to estrus represents 8–9% of the cases except during the months of June to September where they reach 15–20% (Corteel *et al.*, 1964). See Fig. 2.

Gestation--During pregnancy some limited sexual responses may be observed such as nuzzling, sniffing or mounting other females. "False" heats occur, sometimes at irregular, sometimes at 20-day intervals but no detailed study exists on this behavior. Receptivity during gestation appears to be exceptional in the sow. If such a reaction would occur, the intrauterine insemination would probably interfere with embryonic survival.

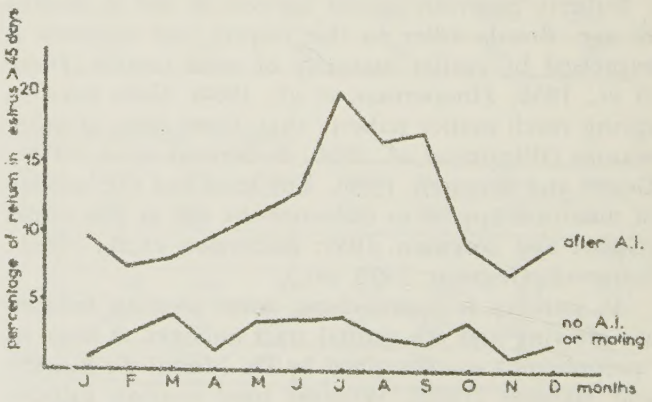

Fig. 2. Seasonal variation in delayed return in estrus.

Postpartum—Postpartum estrus is frequent in sows. Burger (1952) cites only 4 out of 88 having not exhibited estrus within 3 days after farrowing but the percentage varies widely in different studies. Figures obtained by Warnick *et al.* (1950) indicate only 50% and, in our records, 38 postpartum estruses were observed in 104 sows (36%). Warnick *et al.* (1960) observed only 2 out of 18 having ovulated at this estrus and those did not have pigs nursing them. Similarly, Burger (1952) found no pregnancy after mating at this estrus. We may assume that ovulation generally does not occur at this period.

Lactation—During normal lactation period—up to 8 weeks postpartum, there is generally no sexual activity. Burger cites only 4% of suckling sows having exhibited estrus later than immediate postpartum. Crighton (1968) has observed no estrus in his experimental lactating sows when they were continuously kept with their litter.

Weaning—After a normal lactation that lasts 4 weeks or more, postweaning estrus often occurs rapidly. The mode of the distribution is 3–4 days postweaning but the percentage of sows exhibiting estrus at this moment is very different, according to the authors. Burger (1952) observed 64% of Large White sows returning to estrus 3–4 days postweaning compared to 32% in Large Black. Records from our experimental A.I. center indicate that 41.5% of the sows were inseminated within 10 days postweaning. This percentage has increased with parity from 25.4% after the first litter to 55.3% after the 5th litter. A seasonal variation is observed. The percentage in estrus within 10 days postweaning is 53.9% in April and May compared with 39% as an average of the other months (Du Mesnil du Buisson and Signoret, 1968). Some breeders obtain a far better synchronization: 86% on the 3–4 days postweaning (Renoux, 1970). The fertility on postweaning estrus is better than otherwise (63.4% farrowing after one A.I. vs. 51.5%, Du Mesnil du Buisson and Signoret, 1968).

After very early weaning (4–6 days) the return in estrus is not grouped.

When the lactation lasts less than 4 weeks, the returns in estrus are scattered over a larger period of time (Drauschke, 1967). The fertility at the first estrus is impaired when the average lactation period is about 20 days. Moody *et al.* (1966) obtained only 35.2% conception under such conditions.

The Sexual Behavior and its Endocrinological and Ethological Mechanisms*

Sexual behavior involves three major steps:

A physiological (hormonal) signal is transmitted from the gonads to the central nervous system.

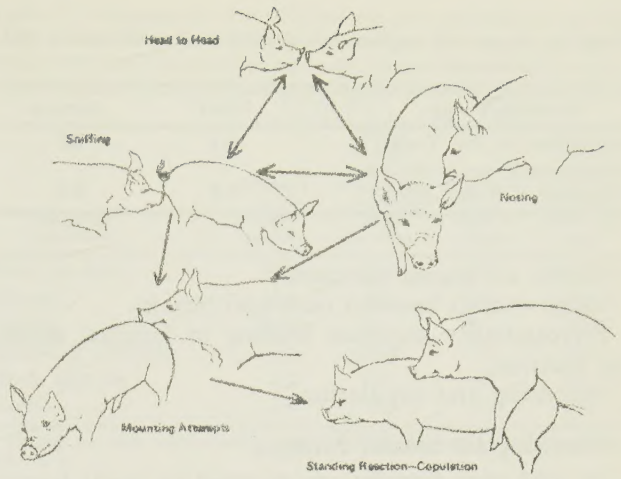

Fig. 3. Ethogram of sexual behavior in swine.

The brain transforms this signal into the sex drive and programs the motor patterns of copulatory activity.

Sensory information allows the initial searching of sexual partners the identification of their physiological stage and releases the adapted motor reactions.

In the present report, after a description of the sequence of the sexual behavior, we shall be concerned with the study of the ethological mechanisms and their endocrine control.

The Sequence of Sexual Behavior

When animals live freely in a herd, the courtship behavior begins long before the first mating. The sequence of events which occur in precopulatory activity is shown in Fig. 3.

The contact between male and female begins generally by a naso-nasal or naso-genital control. When the boar approaches, the female may run from him but he will follow her persistently. During this activity, the boar emits characteristic grunts, often grinding his teeth. Foaming saliva surrounds his mouth. Rhythmic urination may frequently be observed.

If the female stops, the male may nose the flanks, sniff the anogenital region or the head of the female and mount her.

Sometimes a mock fight may occur. The male tries to bite the female's ears and neck, the intensity of the movements being completely different from those of an actual fight.

The characteristic response of the female accepting mating is the standing reaction or mating stance. The sow stands immobile, arching her back and cocking her ears, in a typical posture. When this reaction occurs, the male mounts and copulates quickly.

Ethological Study of the Mechanisms of Sexual Behavior

Sexual behavior in pigs can be divided into four major phases:

* The major part of this chapter was presented to the Society for the Study of Fertility, Bristol, July 1969 and published in J. Reprod. Fert. Suppl. 1970.

Table 6. Motor and exploratory activity during the estrus cycle in the sow.

Physiological stage	Estrus	Anestrus
Movements in the T-maze	8.1	6.3
Average rank out of the pen (groups of 8 or 9 gilts)	2.8	4.6

Search for sexual partners.

Social contact between male and female.

Precopulatory sequence leading to females' standing reaction.

Mounting and copulation.

Searching for Sexual Partners

In wild pigs, females are grouped in small family herds, usually several sows and their offspring. Males join such herds only during the period of reproduction (Mohr, 1960; Gundlach, 1968).

In the domestic boar, the sex drive measured by the average mount latency to a dummy is constant throughout the year. The behavioral sequence appears to be initiated by the female—by changes in her reactions and/or by specific signals emitted during estrus.

Female role—In the domestic gilt, as in laboratory rodents (Slonaker, 1924; Farris, 1944), the spontaneous motor activity increases to about twice the normal level during estrus (Altmann, 1941).

Exploratory activity is increased. The female will use any opportunity to move around. Normal social rank is reduced during heat when the female goes out of its own area. When a sow is placed in an empty pen, both exploratory and motor activity may be measured by the frequency of crossing the limits of the different parts of the pen. During estrus, an increase of this "crossing frequency" is observed (8.1 during estrus vs. 6.3 in anestrus for 5 tests). See Table 6.

Table 7. Gilts mean time in seconds/5 minutes interval in each arm of a T-maze.

Test conditions	Physiological stage of the experimental gilt	Toward the male or the male stimulus	Toward the female or opposite to male stimulus
Male opposed to female (wire fence)	Estrus	206.7[a]	34.3
	Anestrus	70.3	64.5
Male opposed to female (opaque fence)	Estrus	173.9[a]	32.6
	Anestrus	62.2	46.5
Castrated male opposed to female	Estrus	151.7[a]	91.7
	Anestrus	81.2	86.5
Male's recorded courting grunts opposed to nil	Estrus	59.1	46.5
	Anestrus	45.6	48.0
Boar's preputial fluid at 38°C. opposed to warm air	Estrus	43.4	37.6
	Anestrus	53.6	36.1

[a] $P<0.01$.

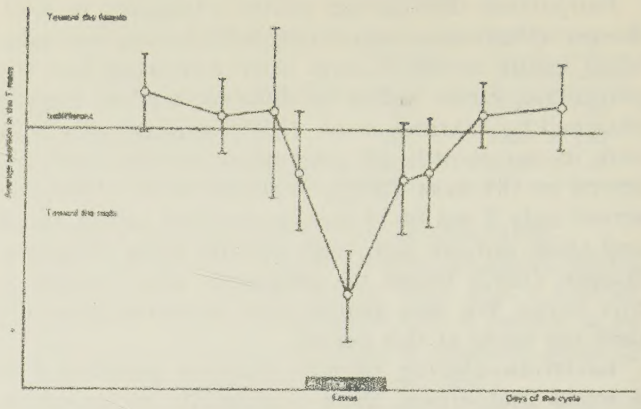

Fig. 4. Reactions of a sow to a boar in a T-maze during the estrous cycle.

When contact is possible, the estrous sow is often observed to go to the boar and to remain close to him (Burger, 1952) Some females actively pursue males on the day prior to estrus (Jakway and Sumption, 1959). T-maze experiments indicate a strong attraction of estrus and proestrus females by the male (Signoret, 1967b). See Table 7 and Fig. 4.

Several sensory informations appear to be involved in the organization of this reaction. When the boar cannot be seen, the attraction is only slightly impaired. Under such conditions acoustic and olfactory cues appear sufficient to release the response. However, the "attraction value" of a postpuberally castrated boar is reduced but persists despite the disappearance of the sexual odor, "courting" grunts and reduced sexual activity. The male's external look may be effective in such conditions (Table 7). After the restoration of his sexual activity, grunts and odor by androgen treatment, the estrous sow's attraction is recovered to precastration level (Fig. 5). But the recorded grunts and the odor of the preputial secretion are without any effect.

The role of previous experience on the attraction of the estrous female to the male was studied in testing animals deprived of social contacts. Gilts were reared from birth in isolation. As adults, they were ovariectomized and tested during heat induced by estrogen injection. They reacted in the T-maze in

Table 8. Effects of social deprivation on the attraction of estrous gilts by the boar.

Test conditions	Physiological stage	Mean time in seconds towards the male or male stimulus		
		Gilts[a]	Gilts[b]	Gilts[c]
Male opposed to female	Estrus	202.8	213.3	206.7
	Anestrus	83.4	33.4	70.3
Boar's preputial fluid at 38°C. opposed to warm air	Estrus	29.2	28.1	43.4
	Anestrus	20.5	16.0	33.6
Boar's recorded courting grunts opposed to nil	Estrus	42.7	54.2	59.1
	Anestrus	55.8	37.9	45.6

[a] Gilts raised in isolation tested before contact with male.

[b] Gilts raised in isolation after contact with male.

[c] Normally reared gilts (control).

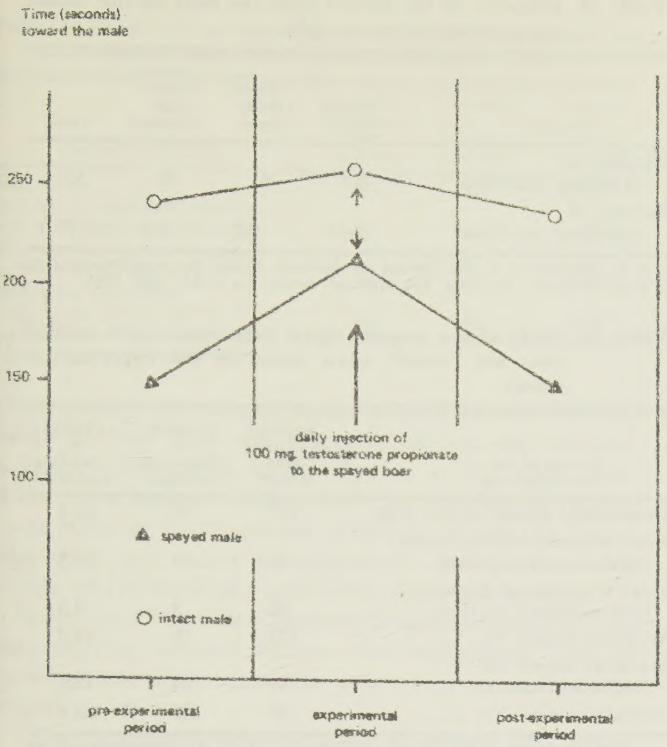

Fig. 5. Influence of androgens on the attraction of the female by the male in a T-maze.

exactly the same way as under socially reared controls (Table 8).

Male role—Detailed observations in the herd indicate that the boar seems to detect estrus females more from behavioral items than from signals passively emitted such as smell or sounds.

Sometimes the boar may pursue an anestrous gilt fiercely and neglect an estrus one for a time. This is confirmed by T-maze experiments (Table 9). The male is only slightly more attracted by the estrous female than by an anestrous one.

Conclusion—If both male and female pigs are always searching for social contact with any conspecific animal, the female role becomes the most important from this respect during the period of reproduction. Her exploratory behavior is largely oriented by signals from the male, the boar being less sensitive to the stimuli from the estrus sow, in our experiments.

In several other mammalian species, similar attraction of the estrus female by the male has been described; in sheep (Inkster, 1957; Banks, 1964; Hulet *et al.*, 1962; Lindsay and Robinson, 1961) and rats (Carr *et al.*, 1962, 1965).

Contact Between Male and Female

During the contact between a boar and a sow, several behavioral patterns take place. The frequency of each of them and their organization in a sequence was observed in small groups of gilts placed in a pen with a boar during a limited period of time (Ca. 3 mn.). The results are presented in Table 10. Head to head, sniffing and nosing are the major patterns

Table 9. Frequency of the different patterns of behavior during social interactions between a boar and a group of gilts.

Nature of interaction	Interactions with estrous gilts		Interactions with anestrous gilts	
	Percent of all inter-actions	Percent of gilts having the interaction concerned with the boar	Percent of all inter-actions	Percent of gilts having the interaction concerned with the boar
Head to head	46.7	97.4	27.2	65.7
Nosing	14.8	36.8	23.1	56.0
Sniffing	28.0	71.1	30.1	58.9
Mounting attempts	6.6	10.5	11.7	33.8
Mock fighting	2.2	21.0	4.8	19.1
Pursuit	1.6	5.3	3.2	12.8

Percent of cases without interaction between the boar and an anestrous gilt: 13.7.

observed during contact with estrous or anestrous females. Pursuit or mock fighting occur infrequently. But often one or several of the major behavioral patterns are lacking in social interaction of the boar and an individual gilt. However, an actual contact takes place in more than 86% of anestrous females.

The initiation of social contact—The patterns of social interaction toward an individual female take place either isolated or in a sequence. In the latter case, the first contact is either sniffing or head to head contact when the female is not in estrus. The last pattern may be sniffing or nosing or, slightly less frequently, head to head or mounting attempts (Table 10). During estrus, head to head appears to be the most frequent as the first pattern of contact.

Organization of the behavioral sequence—The frequency in which each individual pattern is preceded or followed by the others was calculated and shown in Fig. 6. After the first naso-nasal or naso-genital contact, mounting or nosing often take place When the anestrous female has refused male mounting attempts, or pursuit, the behavior of the boar is often nosing or sniffing or, less frequently, head to head. Mock fighting is generally derived from head to head contact.

When the female is in estrus, the organization is exactly the same. We have observed the drop in frequency of mounting attempts owing to the rather

Table 10. Frequency of the behavioral patterns in the initiation and the end of social interaction between a boar and gilts.

Behavioral pattern	Anestrous gilts (percent of all cases)		Estrous gilts (percent of all cases)	
	Initiation of social contact	End of social contact	Initiation of social contact	Last contact before boar mounting
Head to head	43.3	19.1	70.3	7.4
Nosing	12.7	24.3	11.1	25.9
Sniffing	34.5	28.4	18.5	62.9
Mounting attempts	1.6	16.0	0	0
Mock fighting	1.2	2.8	0	4.0
Pursuit	1.2	4.4	0	0

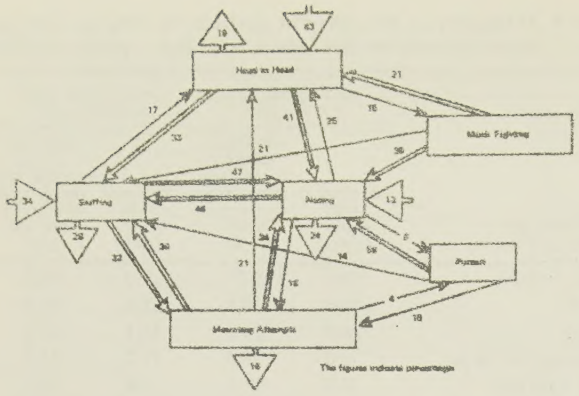

Fig. 6. Schema of the sequence of behavioral patterns during social interaction between a boar and an anestrous gilt.

quick immobilization of the estrous female and a relative decrease in nosing.

Identification of the estrous female by the male—When gilts are presented in a pen to a boar, the first contact between the male and the estrous female occurs at random. The average rank of contact with the boar is similar for estrous or anestrous gilts (3.6 vs. 3.1), the contact latency being slightly reduced (13.1 vs. 18.8 seconds) ($P < 0.05$).

The patterns of social interactions are the same when the gilt is in estrus or not. So, it is possible to infer that in contact with any female, the boar is engaging in courtship behavior. The female's response appears to orient the male's reaction in running away from him after a mounting attempt or an anogenital sniffing or nosing. The increased frequency of sniffing, nosing and naturally of mounting attempts during contact with an anestrous female can be an indication of the techniques used by the male for verification of the negative response of the female.

So, we may conclude that in this experimental situation, the patterns of social contact are essentially similar to those of sexual activity. The response of the female determines the next step of the sequence of reproductive behavior. A similar ritualization of the sexual behavior in social interactions patterns is described in the free living mountain sheep (Ovis dalli) by Geist (1968).

Standing Reaction

The "standing reaction" of the mating stance ends the preliminary phase of sexual behavior by allowing the boar to mount and copulate. The receptive sow stands absolutely immobile, arches her back and cocks her ears. This attitude is invariably concomitant with sexual receptivity in the presence of the male. As they exhibit this reaction, the sows cannot be herded normally and often have to be forcibly carried into their pen if they are not mated.

When an estrus female is touched on the back by an experimenter, she may exhibit the standing reaction even in the absence of the boar. However, only 48% of the estrous gilts do so in the absence of the male. The frequency of response increases from under 40% before the 10th hour of estrus to 60% between the 24th and 36th hours (Signoret, 1961) (Table 11). So, stimuli from the boar are effective in increasing the rate of standing reaction to 100% in estrous females. Olfactory and auditory stimuli appear to be the most important. The standing reaction takes place in 90% of estrous gilts when the boar cannot be seen or touched. The addition of visual and tactile stimuli increased the number responding by 7 and 3%, respectively (Table 12).

Role of auditory stimuli—Broadcasting of tape recorded boar "courting" grunts induces standing reaction in over 50% of gilts negative in the absence of the male. A short sequence of the characteristic grunts continuously repeated is as efficient as the total "courting song" but reducing the rhythm by half reduces the efficiency of the signal. The study of artificial signals shows that both the rhythm and the frequency affect the results (Table 13).

Role of olfactory stimuli—Over 60% of estrous gilts negative to the experimenter exhibit standing reaction

Table 11. Frequency of artificially induced "standing reactions" at various times during estrus.

Interval between the onset of estrus and the test	< 10 hours	From 10 to 24 hours	From 24 to 36 hours	From 36 to 48 hours	From 48 to 60 hours	> 60 hours	Total
Number of estrous gilts tested	465	224	329	156	154	53	1,381
Number of "standing reactions"	181	119	195	74	77	25	671
Percent of "standing reactions"	38.9	53.1	59.2	47.4	50.0	47.2	48.6

J. P. Signoret et F. Du Mesnil du Buisson, Etude du comportement de la truie en estrus. IV Cong. Int. Reprod. Anim., La Haye, Juin 1961.

Table 12. Influence of the stimuli from the boar on the "standing reaction" of estrous gilts.

Stimuli	Sound + Odor	Sound + Odor + Sight	Sound + Odor + Sight + Contact	Total
Number of "standing reactions"	681	51	25	757
Percent of "standing reactions"	90.0	6.7	3.3	100.0

J. P. Signoret et F. Du Mesnil du Buisson, Etude du comportement de la truie en estrus. IV Cong. Int. Reprod. Anim., La Haye, Juin 1961.

Table 13. Study of the acoustic signal (the estrous gilts studied have not "stood" when tested by the experimenter alone).

Nature of the tape recording	Number of estrous gilts studied	Number of "standing reactions"	Percent of "standing reactions"
Unmodified sound of the boar	107	55	51.4
Short sequence of the sound continuously repeated	36	21	58.3
Short sequence of the sound with modified rhythm	32	3	9.3
Artificial sound No. 1	113	15	13.2
Artificial sound No. 1 frequency reduced ½	81	14	17.3
Artificial sound No. 2	58	15	25.8

J. P. Signoret et F. Du Mesnil du Buisson, Etude du comportement de la truie en estrus. IV Cong. Int. Reprod. Anim., La Haye, Juin 1961.

Table 14. Study of the odor (the estrous gilts studied have not "stood" when tested by the experimenter alone).

Olfactory stimulus	Number of estrous gilts studied	Number of "standing reactions"	Percent of "standing reactions"
Boar pen	90	56	62.2
Preputial secretion, warm month (May–September)	60	29	48.3
Not warmed, cold month (November–March)	31	7	22.5
Preputial secretion warmed about 38°C.	80	42	52.5

J. P. Signoret (unpublished).

when placed in a boar's own pen. The odor of the fluid collected from the preputial pouch and warmed at body temperature is as effective as the total odor of the male himself (Table 14). The 5α-androst-16-ène-3-one isolated by Patterson (1968) as giving the "boar odor" to pork meat is apparently involved in this action (Reed-Melrose, personal communication).

Individual reactions—Among 32 gilts studied in 245 tests during natural estrus, the individual rate of standing reactions remained constant from one estrus period to another.

Experience does not affect this response. The standing reaction may be evoked in gilts reared from birth in isolation and the rate of reaction is similar to that of socially reared animals (Table 15).

Conclusion—The behavioral response of the female, i.e., the standing reaction, that ends the precopulatory sequence in allowing the male to mount is released by tactile stimulation but the stimuli from the boar have a cumulative effect to facilitate this response.

Mounting

The female in the mating stance is mounted immediately. In our own records of 202 natural matings, the average mount latency is 43 seconds. Occasionally a boar may mount the female by side or head. In groups of males, homosexual mounting is very frequently observed. Such observations lead to the conclusion that the stimuli releasing mounting are not specific of the estrous female.

The sexual reaction of the male appears rapidly, when presented to a "dummy sow," and involves all the patterns of sniffing, nosing and mounting as in the normal sequence. Similarly, when presented to a simplified dummy, unexperienced young boars react very rapidly by a mounting response (Table 16)—75% mount at the first trial and 78% of them ($^{11}/_{13}$) with erection and coordinated mating response.

Table 15. Immobility reaction data for gilts raised from birth in isolation.

Number of gilts	A	B	C	D	E	F	G	H	Total
Number of tests	13	13	13	13	13	13	13	13	104
Number of standing reactions in the absence of the boar	3	13	6	2	4	11	0	5	44
Percent of standing response	23.1	100	46.1	15.4	30.8	80.4	0	38.5	42.3

Table 16. Mounting reaction in sexually unexperienced young boars reared in groups of males.

Trial n°	1	2	3	4	5
Number of boars exhibiting mounting reaction to the dummy	15	4	1	–	–
Percentage (%)	75	20	5	–	–
Number of boars exhibiting mounting reaction and erection	11	4	1	2	2
Percent (%)	55	20	5	10	10

Experimental A.I. Center–I.N.R.A., Rouillé (86), France. Av. age at first trial 211-225 days (range 185–232 days).

The very high level of reaction of the boar to a dummy leads to the hypothesis that the sexual response is mainly released by visual and tactile cues, the releaser being the overall shape of the female and the immobility. This hypothesis explains the reaction of males to the oversimplified dummies. The same mechanism may account for unadapted behavior, such as homosexual mounting or side or head mounts.

The other visual, olfactory or acoustic information from the estrus female have only a complementary but minor importance. They are not necessary in animals having a high level of sex drive, such as the boar, for releasing the mounting reaction of the male. Such a scheme is similar to the "Torbogen Schema" proposed by Buchlman (1950) for the bull. The other sensory information from the female enhances the sexual responsiveness of the male. The need for different quantity and quality of information according to the species and to the breed may explain the various reactions to dummies or anestrus females.

Discussion and Conclusions

From this analysis of the sexual behavior of pigs, the female is assuming the major role in searching for the male, orienting the social contact in the sexual behavior sequence, and releasing the mounting reaction. Oppositely, the male is always waiting for the characteristic signals given by the female.

Our results indicate differences in the importance of the various sensory stimulations between the phases of sexual behavior. However, in each case, every sense organ receives specific information. Some of them are more important than others (for instance, smell and sound for releasing standing reaction of the female), but all of them have a cumulative action. In the absence of one of the specific signals the behavioral sequence may be less organized.

In other ungulates a similar situation in the males is described by Fletcher and Lindsay (1968) in the ram, Wierzbowski (1959) in the stallion and Hale (1966) in the bull.

The impairment of one or more of the senses does not suppress sexual behavior.

This may lead to an unadpated reaction. For instance, the visual signal presented to a highly sexually motivated male may release mounting of an anestrous female, another male or an inanimate object.

With the use of a domestic species as an experi-

mental animal, the problems arise of possible impairment in the sense organs and of modifications in behavior as a consequence of domestication. However, as far as they have been described, the motor patterns and the various behavioral traits are similar in the wild pig (*Sus scrofa*) and in the Warthog (*Phacochoerus aethiopicus*) and in the domestic swine (Fradrich, 1965). But the frequency of unadapted sexual reaction is much higher in domestic animals and in those living in captivity under zoo conditions.

In both cases, feeding and protection from enemies are supplied by man. The elimination of the fear and hunger drive may account for the increased sex drive. The high level of sexual motivation makes easier the study of reproductive behavior in domestic animals. Their reactions are easily released and observed, even under an experimental situation, but it is necessary to be aware of such conditions in order not to oversimplify the sensory mechanisms of sexual arousal or to overestimate the role of sex in social interactions.

Endocrine balance

The Male

No detailed study of the endocrine balance of the sexual behavior has been done in the boar. Occasional observations show that the postpuberally castrated male may exhibit the complete sequence of sexual behavior in the presence of a receptive female, including erection and vaginal penetration as long as two years postcastration. Androgen therapy (0.5 mg./kg./day) enhances the sexual excitement and restores the "attractive" value for the estrous sow.

The Female

As in other female mammals, no sexual activity can be observed in the ovariectomized sow. The endocrine secretion of the ovary is the signal that triggers the sexual activity.

Endocrine secretion during normal cycle—Estrogen secretion takes place immediately before the onset of heat and its level falls rapidly and is very low during estrus (Lunaas, 1965; Raeside, 1963). Plasma progesterone level reaches a minimum 1–2 days before sexual receptivity and increases 2–3 days after the end of estrus (Stabenfeldt *et al.*, 1969).

Induction of estrus in ovariectomized females—Artificial endocrine balance in ovariectomized females allows the study of the qualitative and quantitative effect of the steroid hormones involved.

Estrogen: One estrogen injection induces normal sexual behavior. This desponse is repeatable during one year of injections at 21-day intervals. In our experiments the responses appear with an I/M injection of .25 mg. of estradiol benzoate. With .5 mg., estrus is observed in all the animals treated. The duration of heat increases logarithmically with the dose of estrogen (Fig. 7) but the delay between injection and the onset that induces the spontaneous duration of estrus was .6-.7 mg. of estradiol benzoate (Signoret, 1967). Such value is high compared with that observed

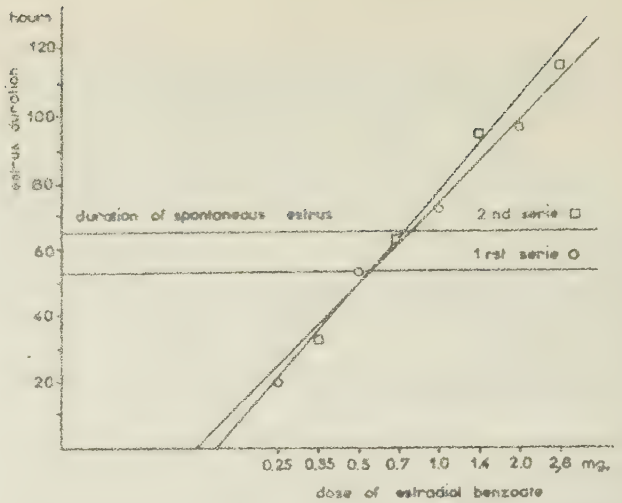

Fig. 7. Action of the dose of estrogen on estrus duration in ovariectomized gilts.

in sheep (25 microg., Robinson, 1954) and in cattle (400 microg., Carrick and Shelton, 1969) but it does not result as a refractoriness acquired by the injection of a high dose of estrogen as described in heifers by Carrick and Shelton (1969), as a first injection of 100 microg. post-ovariectomy is without any effect.

Progesterone: The synergistic action of progesterone and estrogen reported in the ewe by Robinson (1954, 1956) does not exist in the sow but when given simultaneously with or after estrogen, progesterone may totally inhibit sexual behavior (Signoret, 1968).

Recent results show that the period when progesterone may inhibit the sexual behavior response is limited to the 24 hours following the estrogen injection (Signoret, unpublished data, Table 17).

Drugs used for ovulation control inhibit estrus behavior only if they have a progestational action. FGA-treated ovariectomized gilts do not respond to estrogen injection. Oppositely methallibure has no inhibtory action on estrus induced by estrogen injection in ovariectomized gilts or after PMSG-induced ovulation in intact ones (Polge and Day, 1969) (Table 18).

Androgens: Androgens are reported to induce sexual activity in females of several species, including human. In ovariectomized gilts a normal sexual behavior response is induced by testosterone proprionate injection. A dose response relation appears in the same way as for estrogen (Table 19). A similar inhibi-

Table 17. Effect of progesterone on estrus response induced by estrogen in ovariectomized gilts.

Interval between estrogen and progesterone injections	Dose of hormone		Number of cases	Number of estrus response	Rate of estrus response
	Estradiol benzoate (mg.)	Progesterone (mg.)			
0–12 h	1	40 + 40	12	0	0
12–24 h	1	40 + 40	24	0	0
24–36	1	40 + 40	12	2	16.6
Control	1	–	24	22	91.7

Table 18. Estrus reaction after estrogen injection (1 mg.) in relation with ovulation-inhibiting drugs.

Treatment	Number of cases	Number of estrus response	Rate of estrus response
Control	12	12	100
FGA 40 mg. vaginal sponge	12	1[a]	8.3
Methallibure 40 mg./day	12	12	100

[a] Vaginal sponge lost immediately after injection.

Table 19. Effect of androgen injection in ovariectomized gilts.

Hormone	Dose (mg.)	Number of cases	Number of estrus response	Rate of estrus response	Av. duration of heat (hours)
Estradiol benzoate	1	10	9	90	79.3
Testosterone propionate	30	10	9	90	61.3
Testosterone propionate	60	10	10	100	82.8

tion of estrus response can be obtained by progesterone.

Quantitative variations in response: Duration of the response is controlled by other mechanisms than the dose of estrogen. With a constant dose of estrogen in ovariectomized females, we observe a seasonal variation in the duration of the sexual response in the same way as with spontaneous estrus in intact ones (Fig. 8).

Individual variations in the duration of responses are similar in spontaneous estrus and after estrogen treatment. With a constant dose in spayed females, heat lengths under these two conditions are positively correlated ($r = 0.685$) (Fig. 9).

Qualitative aspect of the sexual behavior induced by hormonal treatment: The attraction toward the boar is similar to what is observed during spontaneous estrus in ovariectomized females. However, increasing the dose of estradiol benzoate injected to induce heat

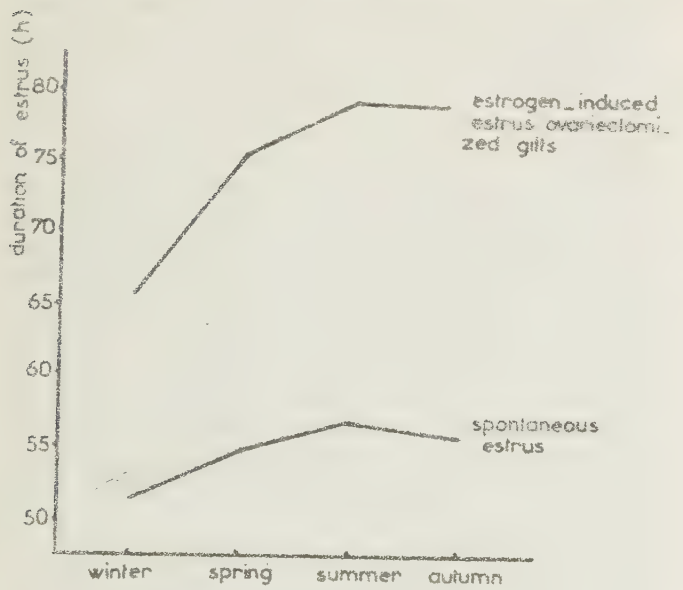

Fig. 8. Seasonal variations in the duration of estrus.

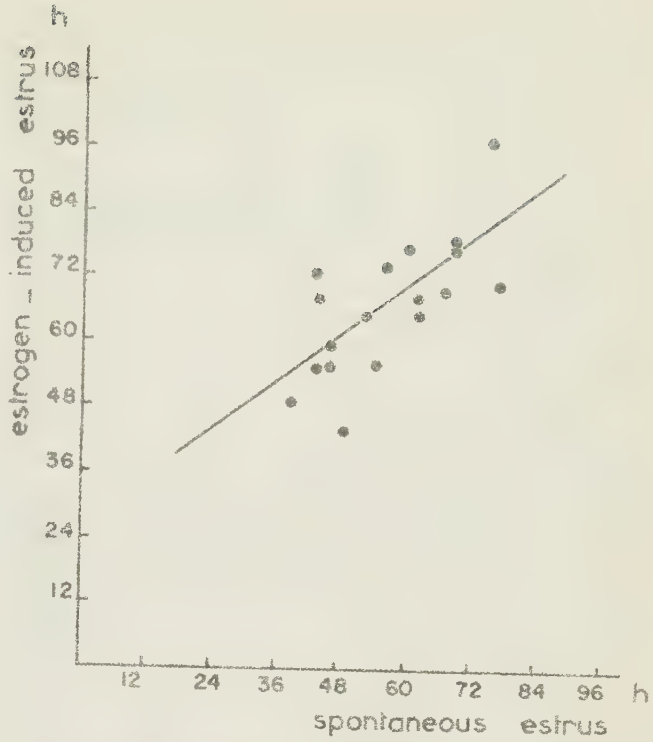

Fig. 9. Duration of spontaneous and estrogen-induced estrus in the same animals.

shows a tendency to enhance, although nonsignificantly, the attraction towards the boar (Table 20).

The sexual sequence appears similar after estrogen injection or spontaneously as indicated by the first results of observations actually in progress.

The immobility reaction is not changed. The individual rate of standing reaction remains constant from one estrus period to another. During spontaneous heat before ovariectomy or after estrogen injection later (Table 21) increasing the dose of estradiol benzoate does not affect the reaction rate (Table 22).

Conclusion—A physiological signal: Presence in the blood flow of estrogen (or androgen) during a limited period of time triggers the complete integrated neurological mechanism of sexual behavior. The amount or even the nature of the hormonal signal can only influence the duration of the phenomenon, not the details of its realization—frequency or intensity of patterns, individual or seasonal variations, etc.—that appear predetermined and probably under genetic control.

Relationships Between Behavior and Reproduction

The results of the study of sexual behavior may be of some use for some breeding under two main aspects:

Table 20. Effect of the dose of estrogen injected in ovariectomized gilts to induce heat on attraction by the boar.

Test conditions	Dose of estradiol benzoate (mg.)	Mean time in records toward the male
Male opposed to female	0.75	226.7
	1.5	240.0
	3.0	244.6
Intact male opposed to castrate	1.0	128.3
	2.0	170.1

Table 21. Immobility reaction data for gilts raised in heterosexual groups.

	Before ovariectomy (32 animals)	After ovariectomy, estrus induced by estrogen injection: Low reaction group (15 animals)	Average (6 animals)	High (11 animals)	Total (32 animals)
Number of tests	245	311	115	227	653
Number of standing reactions in the absence of the boar	106	11	38	219	268
Percent of standing reactions of positive response	43.3	3.6	33.0	96.4	41.05

Table 22. Influence of the dose of estrogen on the standing reaction.

Conditions			Percent of standing reaction in the absence of the boar
Intact gilts natural estrus			23.3
After ovariectomy	Estrus induced by injection of estradiol benzoate	0.5 mg.	25.8
		1.0 mg.	28.8
		2.0 mg.	28.2

To utilize some patterns of sexual behavior to develop the techniques of artificial insemination, semen collection in the male, test of estrus and of gestation in the female.

To use the influences of behavioral items on the mechanisms of reproduction to improve the techniques—external effects on estrus control, influence of various stimuli on fertility, etc.

Sexual Behavior and Development of Artificial Insemination Techniques

Semen Collection—Mounting reaction

The teaser—Although several authors have first used as a teaser an estrous sow or a castrated male (Gotze, 1949; Herrick, 1949; Baier and Grauvogl, 1959), the nature of visual stimuli eliciting the sexual reflexes in the boar allowed the use of very simple dummies. The various models were reviewed by Rothe (1963). Main types are:

Compact models, the overall shape of which is more or less similar to that of the sow, with the artificial vagina placed in it. Sometimes it is covered with a pigskin with hairs and equipped with a stuffed head (Gotze, 1949; Hahn, 1958; Pasztor, 1955; Oshin *et al.*, 1959; Rothe and Radtke, 1961).

Simplified models adapted for an easier collection when the artificial vagina is held by the hand of the collector. (Rodolfo, 1934; Glover, 1955; Polge, 1956; Ito, 1948; Paredis, 1961; Aamdal *et al.*, 1958).

The effectiveness of the dummies appears very good. Their value to release the sexual response as measured by the mount latency is not very different from that of the normal stimulus, *i.e.*, the estrus sow: 1.2 min. in 3,263 cases (Signoret, 1969), 130 seconds (Wierzbowski and Wierzchos, 1968) for reactions to a dummy, 43 seconds (202 cases) (Signoret, 1969), 75% of the cases in less than 200 seconds (Jakway and Sumption, 1959).

Table 23. Influence of mount latency on semen composition.

Mount latency	Less than 2 mn.	2–4 mn.	Over 4 mn.
Number of cases	2,538	635	95
Average volume (ml.)	302	292	273
Average sperm number x 109	99	107	105

Training of young boars for semen collection—Young boars react rapidly to the dummy but the main difficulties appear to be due to the fear of the male being approached by the man when mounting the dummy. In our experience with 20 young boars trained in 1969, 5 were not collected at their first mount due to the reaction of fear when approached but this was overcome in 1–4 trials. As an average, in the experimental A.I. station of the I.N.R.A., the age at the first collection for 76 boars was 226 days and the weight 118.5 kg. The use of dummies with incorporated vagina may be of some use for very shy animals. The fear reactions are minimized when the boars are accustomed to the presence of the man and when the training takes place in their own pen.

Enhancing the sexual response in boars—Several techniques are cited to enhance the sexual reaction either for slow males or to train boars to react to the dummy. However, their effectiveness has not been scientifically studied. Among them are spreading of sow urine or boar semen on the dummy, presence of another male mounting, etc. Rothe (1963) describes an increase in sexual excitement of the boar when the dummy is equipped with a stuffed head.

The presence of a living pig is often reported to increase the sexual excitement of the boar. Smidt (1965) describes use of a dummy where a young pig may be placed in a cage, allowing an easy collection in the presence of a living teaser animal.

The use of exogenous hormones was proposed by Ellendorf *et al.* (1970) to advance sexual maturity. The treatment FSH-LH-Testosterone stimulates sexual behavior but has little effect on sexual maturity.

Effect of sexual excitement on semen composition—The effect of sexual preparation before semen collection has not been studied in boars as it has in bulls. There is no significant improvement of the composition of the semen when the mount latency increases (Table 23). However, Rothe (1963) observed an increase of 26–28% in the volume of semen obtained when using a dummy resembling a sow and equipped with a stuffed had as compared with a simplified one.

The ejaculation

The fact that pressure is the main stimulus eliciting ejaculation in the boar, led to a simplification of the

methods of semen collection. Rodolfo (1934), Rodin (1940) were using a modified bull type of artificial vagina, in which changes in pressure were induced by a rubber bulb. This model evolved with the addition of a metal spiral placed on the inner rubber sheath and where the boar's penis was fixed during ejaculation (Niwa, 1959; Melrose and O'Hagan, 1958).

In the method of Aamdal *et al.*, 1959, the penis was fixed by the hand. In all these techniques, warm water was used to obtain a temperature of about 40°C. Simpler methods derived from that described first by McKenzie (1931). The penis of the boar is directed into a thin-walled rubber tube around which the fingers are held. The pressure applied on the penis is sufficient to elicit ejaculation. A similar method was described by Ito *et al.* (1948) but grasping the penis with the gloved hand without any artificial vagina is as effective.

Estrus Detection

When the sow is hand mated or artificially inseminated, the herdsman has to identify the proper moment for reproduction.

The safer and the more accurate method is the use of a teaser boar. With groups of 4–8 sows, the best results are obtained when the male is placed first in the test pen so that he becomes accustomed to the environment. With a normally active boar, 5 minutes is enough to allow contact of the male with each female. Vasectomy is not necessary as the delay between mounting and the onset of mating is long enough to allow the female to be removed. The same boar may be used for a long time provided the herdsman is aware not to hurt him during separation from the sow.

This technique has to be used for research or experimental work but may seldom be applied under the conditions of organization in commercial breeding.

Various changes in anatomy or behavior are noted by breeders—restlessness, loss of appetite, typical grunts, changes in coloration of vulva, etc. Since they are not reliable enough separately, when observed together, they allow the trained herdsman a rather good identification of the estrous sow. The "riding" test—the herdsman sitting astride the sow's back—is well-known by pig breeders and was proposed as a test for the moment of artificial insemination (Burger, 1952; Madden, 1959; Aamdal and Hogset, 1957; Willems, 1961; Holt, 1959; Hoffmann, 1964; Van Putten, 1965, etc.).When positive it is an objective and doubtless sign of estrus. However, in the absence of the boar, this reaction cannot be released in every estrous sow (Signoret, 1961; Schenk, 1967).

In the laboratory, the average reaction rate observed was 671/1,381 = 48.6% for gilts, with a maximum 24–36 hours after onset of heat of 60%. In the field work of A.I., we have observed 4,177/6,708 = 70.4% for gilts and 10,557/13,037 = 81% for sows. The higher figures obtained in the field may be due to elimination of negative animals.

Similar rates are observed in field A.I. in Great Britan—80% positive females (Melrose, personal communication).

The possibility of increasing the rate of immobility reaction by the use of stimuli from the male has been tried, using olfactory or acoustic signals (Hofman, 1964; Wettke, 1964), magnetic tape recording (Smidt, 1965), artificial sound (Jacobsson, 1962; Smidt, 1965; Wettke, 1964). But despite the positive results obtained in those studies and others that we have done ourself, no method simple enough to be applied in the field has been reported. However, the recent identification of the 5α-androst-16-ène-3-one as the effective sexual odor in the boar by Patterson (1968) led to a field trial of this compound to induce immobility in sows as a test for artificial insemination (Reed, personal communication). If positive results are obtained, this may provide a good way to improve heat detection in the sow.

Soon, however, the importance of this problem may be completely changed if ovulation control becomes accurate enough to allow field insemination without estrus detection.

Tests of Pregnancy

The absence of recurrent estrus is generally used as the earliest test for pregnancy. With artificial insemination, the "nonreturn" rate is the index to measure the efficiency of the techniques. In the pig, sexual activity during pregnancy is exceptional but long-lasting anestrus following unsuccessful insemination is rather frequent. The nonreturn rate is not an accurate measure of the efficiency of A.I. in swine. The difference between nonreturn rate and farrowing rate is not only important but it varies according to the season and the behavioral reaction of the female (Table 24, etc.).

The inhibition of response to estrogen by progesterone has led Andrae *et al.* (1969) to propose a pregnancy diagnosis test using an injection of estro-

Table 24. Value of nonreturn rate as a test of pregnancy.

Differences between nonreturn and farrowing rate	
Number of artificial inseminations	3,296
% nonreturn after 30 days	79.3%
% nonreturn after 60 days	73.4%
Farrowing rate	59.0%

Variations in the difference, nonreturn and farrowing rate

Cause of variation		Number of A.I.	Rate of delayed return in estrus (Over 45 days)
Season	June–September	6,847	18.2%
	October–May	13,302	10.2%
Behavioral reaction	Immobile	5,554	8.4%
	moving	1,626	14.1%
Number of A.I.	First	4,529	11.0%
	"return"	2,712	7.4%
Delay weaning-insemination	Under 10 days	1,127	5.7%
	Over 10 days	2,580	12.7%

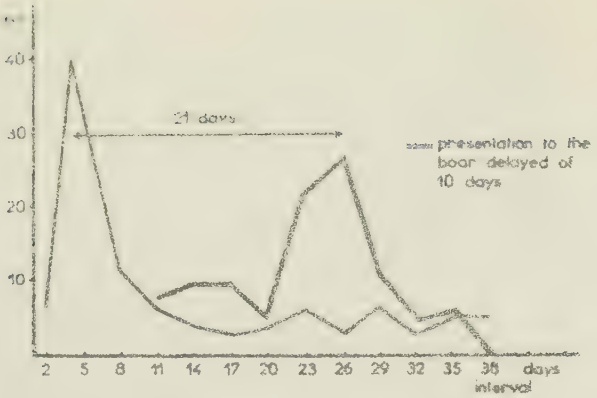

Fig. 10. Interval between transport and onset of estrus in gilts.

gen + androgen (Gravignost) (5 mg. testosterone enanthate + 2 mg. estradiol valerianate) on day 10–30, nonpregnant sows exhibiting estrus within 5 days of injection but this test would fail to detect pseudopregnancy with persistent corpora lutea.

Influence of Sexual Behavior on Reproduction

Estrus Control

When gilts around the age of puberty are transported and changed to the breeding herd, estrus often occurs within a few days. In the herd of the laboratory of reproductive physiology, we observed 277/1,043 gilts, between 90–110 kg., exhibiting estrus on 4–6 days after their arrival in the experimental piggery. Such a synchronization is not the "male effect" as described in sheep (Schinckel, 1954). When the presentation to the boar is delayed by 10 days the peak of estrus is not changed (Fig. 10). The stress appears to trigger the hormonal discharge inducing the puberty. We may suppose that this reaction occurs in "prepuberal" gilts.

The average percentage of prepuberal gilts is similar to that of grouped puberty and when the transport stress is applied to gilts with delayed puberty it is inefficient (Martinet, unpublished data). A better knowledge of this mechanism is able to make easier ovulation control in gilts.

After weaning, a spontaneous grouping of estrus is observed and fertility is better than later—65.01% farrowing rate when A.I. is performed within 10 days after weaning (1,618 sows) vs. 52.28% for A.I. later than 10 days postweaning (2,157 sows).

But the percentage of animals grouped varies considerably from 45% in small herds (13,049 A.I. in the experimental A.I. center of the I.N.R.A.) to 90% and more in some other herds. The technique of weaning (complete separation from piglets, severe fasting for 3 days) interferes with the results. Under the best conditions, such a technique allows an excellent synchronization of estrus. In one herd (Renoux, 1970) weaning of 88 sows on Friday resulted in 42 matings on Tuesday and 34 on Wednesday. Only 1 occurred on Sunday.

During lactation, several authors have succeeded in inducing estrus 20–30 days postpartum in separating the piglets 12 hours/day from the sow (Burger, 1952; Crighton, 1968). As lactation is not impaired, we may suppose the possibility of an interaction of the material behavior with the endocrine mechanisms similar to what occurs during lactation anestrus in sheep and cattle where suckling prevents return in estrus at the same moment as in females milked.

As for puberty, a better knowledge of the physiological and psychological mechanisms at this stage would be very useful in the development of ovulation control techniques and for increasing the rhythm of reproduction.

Table 25. Influence of the presence of the immobility reaction on the farrowing rate.

	Positive		Negative	
Animals	Number of A.I.	Farrowing rate	Number of A.I.	Farrowing rate
Gilts	4,717	50.16%	1,986	30.36%
Sows	10,557	61.80%	2,480	35.60%

Role of the Sexual Behavior Sequence on Fertility

The farrowing rate after natural mating is generally very high—77–88% (Berge, 1941), 73–95% (Holt, 1949), 82% (Jakobs, 1959), 94% (Schenk, 1967), etc. Compared with these figures the results after A.I. are lower—58.3% (19,073 A.I.) in the experimental center of Rouillé (France). However, when inseminations are performed in large herds after heat detection by a teaser boar, the farrowing rate with the same boars and techniques reaches 70–85%.

In large herds of D.D.R. with estrus detection by boars, the comparison of natural mating with A.I. in large herds has given similar farrowing rates (80 and 76% vs. 83 and 73%) (Busch, 1968). We may suppose that the problem of heat detection and/or the role of the presence of the male may account for such a difference.

Immobilization and fertility—When the sow is presenting a positive reaction to the "riding test," the farrowing rate obtained after A.I. is always higher than with a negative response (Table 25).

However, when sows are naturally mated after the riding test in the absence of the boar, Schenk (1967) observed no difference in farrowing rates. We may suppose that physiological events occurring in relation to the immobility reaction allow a better fertilization. The mechanisms involved have not been studied. However, Docke and Worch (1963) observed that the uterine contractions increase considerably during the preliminary phases of the sexual behavior sequence—approach of the boar, sniffing and mounting.

Effect of the stimulation of natural mating—During natural mating the sensory stimuli of copulation may influence the female's physiological reactions. The duration of sexual receptivity is not changed when the sow is mated or artificially inseminated (Burger,

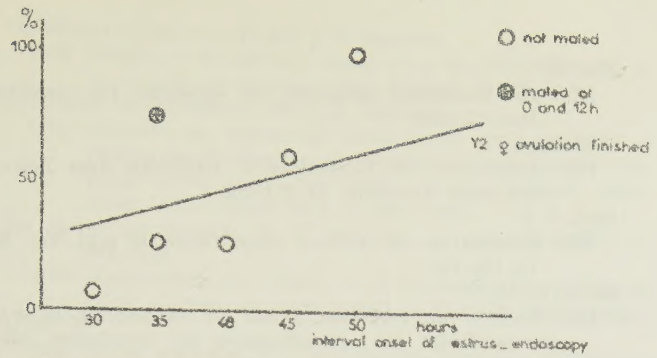

Fig. 11. Influence of mating on the evolution of ovulation.

1952; Signoret, 1967). Although the sow is a spontaneous-ovulator, mating was reported to change the course of ovulation (Lebedev and Pitkianen, 1951, 1955; Lebedev, 1957). Visualization of the ovary by coelioscopy confirmed that mating early in estrus advances the moment of ovulation (Fig. 11). (8/12 complete ovulation 35 hours after onset of heat and two matings at 0 and 12 hours).

Conclusions

In the field of reproduction as it relates to animal behavior, research and practical application developed in three stages:

1. *Empirical observations* of generations of herdsmen and breeders were largely sufficient to allow a first development of new techniques in which behavioral reactions of the animals were involved. This was the case of semen collection and heat detection for artificial insemination.

2. *Scientific studies* were generally undertaken "a posteriori." They first gave a verification of the value of already-used techniques but soon the results offered new possibilities. We are just starting with this stage and have made developments in techniques already in use. Examples are a more rational "management" of the sexual behavior of males for optimum semen production and, for the female, improvements of the "riding test" by the use of stimuli.

Physiological correlates of behavioral reactions: We have for a long time considered animals' physiology as being the interrelation of hormonal and biochemical mechanisms, each step of which we are able to isolate and repeat under artificial laboratory conditions. This has led to the amazing development in knowledge of physiology and its practical applications. But now we have reached a point where the role of external factors and specially the sensory informations of the natural behavioral sequence have to be stressed. In the field of swine reproduction, the identification of the physiological consequences of the sexual behavior sequence is of major importance in the development of A.I. techniques (importance of immobility reaction and the stimuli of mating).

The psycho-physiological mechanisms involved in lactation anestrus, postweaning estrus and the role of stress could help improve methods of ovulation control.

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